Causes and mechanisms of synchronous succession trajectories in primeval Central European mixed *Fagus sylvatica* forests

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Running headline

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Abstract

1. Natural succession trajectories of Central European forest ecosystems are poorly understood due to the absence of long-term observations and the pervasive effects of past human impacts on today's vegetation communities. This knowledge gap is significant given that currently forest ecosystems are expanding in Europe as a consequence of global change.

2. Annually laminated sediments were extracted from two small lowland lakes (Moossee 521 m a.s.l.; Burgäschisee 465 m a.s.l.) on the Swiss Plateau. We combine high-resolution palaeoecological and quantitative analyses to assess changes in vegetation during the Neolithic. We test for regionally synchronous land-use phases and plant successional patterns that may originate from complex interactions between human and climatic impacts.

3. Mixed *Fagus sylvatica* forests dominated the Swiss Plateau vegetation over millennia. During the period 6,500–4,200 cal year BP, pronounced forest disruptions accompanied by increased fire and agricultural activities occurred at *c.* 6,400–6,000 cal year BP, 5,750–5,550 cal year BP, around 5,400 cal year BP and at 5,100–4,600 cal year BP. Biodiversity increased during these land-use phases, likely in response to the creation of new open habitats. After decades to centuries of land-use, arboreal vegetation re-expanded. In a first succession stage, heliophilous *Corylus avellana* shrubs were replaced by pioneer *Betula* trees. These open arboreal communities were outcompeted within 150–200 years by late successional *F. sylvatica* and *Abies alba* forests. Most strikingly, cross-correlations show that these successions occurred synchronously (±11 years) and repeatedly over large areas (>1,000 km^2) and millennia.

4. *Synthesis.* First notable human impact shaped the primeval mixed *F. sylvatica* forests in Central Europe from *c.* 6,800–6,500 cal year BP on. Agrarian societies were susceptible to climate changes and we hypothesize that climate-induced, simultaneous agricultural

expansion and contraction phases resulted in synchronous regional forest successions. Currently forests are expanding in Central Europe as a result of land abandonment in marginal areas. Our results imply that mixed *F. sylvatica* forests with *A. alba* and *Quercus* may re-expand rapidly in these areas, if climate conditions will remain within the range of the mid-Holocene climatic variability (with summers *c.* +1–2° C warmer than today).

KEYWORDS

Biodiversity, Charcoal, Climate change, Cross-correlations, Fire ecology, Forest resilience, Non-pollen palynomorphs, Palaeoecology and land-use history, Pollen, Swiss Plateau

1. INTRODUCTION

European forest ecosystems have expanded over the last decades in response to global change involving increasing land abandonment in marginal regions (FOREST EUROPE, 2015). Most forests are still intensively managed and natural succession is restricted to a few remnant areas (Ellenberg, 2009; Kaufmann, Hauck, & Leuschner, 2018). The direction of ongoing forest change is difficult to assess since the projections are mostly based on short-term observations alone (Willis & Birks, 2006). After disturbance, forest vegetation spontaneously tends towards a late successional stage, which is often unknown because modern forests have been strongly altered by humans over centuries to millennia (Ellenberg, 2009; Puhe & Ulrich, 2001). Studying long-term successional patterns in the past (>200 years) provides unique information about vegetation dynamics under quasi-natural conditions, that may help assess future vegetation dynamics (Foster, Schoonmaker, & Pickett, 1990). Specifically, the assessment of vegetation shifts at the onset of the Neolithic, when humans gradually became sedentary in Europe (Guilaine, 2015; Müller, 2015; Schier, 2015). This period

provides insights into successional patterns of moderately disturbed forests that were only marginally shaped by human activities under environmental conditions comparable to today (Kalis, Merkt, & Wunderlich, 2003). That information is crucial for nature conservation and forest management in protected areas such as national parks (Feurdean & Willis, 2008; Lindbladh, Niklasson, Karlsson, Björkman, & Churski, 2008; Valsecchi, Carraro, Conedera, & Tinner, 2010).

Previous palaeoecological studies in Central Europe have nicely illustrated that early successional (e.g. pioneer herbs, *Corylus avellana*, *Betula*) and late successional stages (*Fagus sylvatica*, *Abies alba*) oscillated more frequently and pronouncedly after 6,500 cal year BP (Ammann, 1989; Becker et al., 2006; Kleinmann, Merkt, & Müller, 2015; Rey et al., 2017). Statistical analyses confirmed that prominent changes in vegetation were directly linked to land-use (Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Rey et al., 2013; Schwörer, Colombaroli, Kaltenrieder, Rey, & Tinner, 2015; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). Fires were commonly used to open landscapes to create space for settlements, pastoral and arable land (Jacomet et al., 2016; Tinner, Conedera, Ammann, & Lotter, 2005), primarily disadvantaging late-successional trees and favouring the expansion of heliophilous herbs and shrubs (Conedera, Colombaroli, Tinner, Krebs, & Whitlock, 2017; Tinner et al., 2000). Many studies numerically show that land-use substantially increased open land biodiversity over the long-term (Colombaroli, Beckmann, van der Knaap, Curdy, & Tinner, 2013; Colombaroli & Tinner, 2013; Giesecke, Ammann, & Brande, 2014). However, one crucial question still remains: were the marked vegetation changes spatially synchronous? This question is important to assess the underlying causes of ecosystem change. Synchronism would speak for a superimposed forcing such as climate (i.e. precipitation and/or temperature changes) or, perhaps less likely, concerted cultural activities (Berglund, 2003; Tinner et al.,

2003), whereas diachronism would rather point to spatio-temporally randomized land-use phases of local autarchic societies that were acting independently from each other (Rösch & Lechterbeck, 2016). Until now, it was impossible to test these competing hypotheses because available records lacked temporal precision and resolution (Berglund, 2003; Tinner et al., 2003). In this study, we aim to resolve this long-standing question with high-resolution palaeoecological and time-series analyses that rely on varved sediment chronologies reaching exceptional temporal precision of *c.* ±20–50 cal years (Rey et al., 2018). The overarching goal of the study is to explore the nature of re-occurring broad-scale successional patterns in mixed beech forests after moderate human impact to refine existing projections of future forest transformations (Bugmann et al., 2015; Ruosch et al., 2016) under global change conditions that are currently triggering forest expansions in Central Europe and adjacent regions.

2. MATERIAL AND METHODS

2.1. Study sites

The study area is located on the western Swiss Plateau in southern Central Europe (Figure 1). Moossee is a small lake close to the city of Bern at 521 m a.s.l. (47°1'17.0''N, 7°29'1.7''E). The lake has a maximum water depth of 22 meters and a surface area of 0.31 km^2. Burgäschisee is a small lake further to the northeast (*c.* 25 km from Moossee) at 465 m a.s.l. (47°10'8.5''N, 7°40'5.9''E). It has a maximum water depth of 31 meters and a surface area of 0.21 km^2. Both lakes are eutrophic today with anoxic waters in the hypolimnion (Guthruf, Zeh, & Guthruf-Seiler, 1999). The present climate is temperate with mean annual temperatures of 8.8°C and an annual rainfall of 1,059 mm at Moossee (data from Bern/Zollikofen at *c.* 3 km distance, MeteoSwiss, 2017). At Burgäschisee, it is slightly warmer and wetter with mean annual temperatures of 9.1°C and an annual rainfall of 1,088 mm (data from Koppigen, at *c.* 6 km

distance, MeteoSwiss, 2017). The current vegetation at both lakes is dominated by mixed *F. sylvatica* forests on the surrounding hills and scattered mixed *Alnus glutinosa-Fraxinus excelsior* stands on the lake shores. Most of the flat areas around the lakes are intensively used for agriculture. The region has been important for agricultural activities for millennia as indicated by frequent local archaeological findings dating back to at least 6,800-6,500 cal year BP (Hafner, Harb, Amstutz, Francuz, & Moll-Dau, 2012; Harb, 2017; Wey, 2012).

2.2. Corings and chronologies

In 2014, three parallel sediment cores at Moossee and two parallel sediment cores at Burgäschisee were retrieved with a UWITEC piston corer (core diameter: 9 cm, core length: 200 cm) in deep parts of the lakes. A total of 7 m of lake sediments were sampled at each site covering *c.* 9,000 years. For this study, we focus on the Neolithic to Early Bronze Age period (6,500−3,800 cal year BP) during which the sediments are annually laminated (i.e. varved) at both lakes (see Rey et al., 2018).

The Moossee chronology is based on 27 terrestrial plant macrofossils and varve counts (Rey et al., 2018). The program OxCal 4.3 (V-sequence; Bronk Ramsey, 1994, 1995, 2001; Bronk Ramsey, van der Plicht, & Weninger, 2001) and the IntCal13 calibration curve (Reimer et al., 2013) were used to estimate the age-depth model (Figure 2a). The Burgäschisee chronology is based on 22 terrestrial plant macrofossils and basic assumptions about the sedimentation rates from a previous chronology (Rey et al., 2017, 2018). Here, the program OxCal 4.3 (U/P-sequences; Bronk Ramsey, 1994, 1995, 2001, 2008; Bronk Ramsey & Lee, 2013) and the IntCal13 calibration curve (Reimer et al., 2013) were used for the estimations of the age-depth model (Figure 2b). Both records indicate fairly regular sedimentation rates for the investigated time interval with an average of 26 years/cm at Moossee and 18.7 years/cm at Burgäschisee.

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138 **2.3. Pollen, macrofossil, non-pollen palynomorphs and charcoal analyses**

139 All palaeoecological analyses were conducted on the same cores and for the same sample
140 depths (Moossee: 312 samples, Burgäschisee: 308 samples). We applied a contiguous,
141 approximately constant year sampling (10 ± 2 years/sample). For all microscopic analyses
142 (pollen, non-pollen palynomorphs (NPPs), microscopic charcoal), samples of 1 cm^3 were
143 treated with HCl, KOH, HF, acetolysis, sieved with a mesh size of 500 µm and mounted in
144 glycerine following standard palynological methods (Moore, Webb, & Collinson, 1991).
145 *Lycopodium* tablets (University of Lund batch no. 1031 with 20,848 ± 3,457 spores per tablet
146 for Moossee and University of Lund batch no. 177745 with 18,584 ± 1,853 spores per tablet
147 for Burgäschisee) were added prior to the chemical treatment to estimate microfossil
148 concentrations (Stockmarr, 1971). We used palynological keys (Beug, 2004; Moore, Webb, &
149 Collinson, 1991), photo atlases (Reille, 1992) and the reference collection at the Institute of
150 Plant Sciences (University of Bern) to identify pollen and spores under a light microscope at
151 400× magnification. Phase contrast under 1,000× magnification was used to separate various
152 Cerealia-types (*Hordeum*-type, *Triticum*-type; Beug, 2004). The minimum number of
153 terrestrial pollen grains counted per sample was 500 with a total of 132 (Moossee) and 113
154 (Burgäschisee) identified terrestrial pollen types. The results are presented as percentages of
155 the terrestrial pollen sum (Figures 3 and 4), in which we excluded spores, pollen of aquatic
156 plants and other microfossils (e.g. stomata, algae cells). Pollen can be dispersed by wind over
157 large distances (up to 50 km) and generally represents extra-local to regional vegetation
158 dynamics (Conedera, Tinner, Crameri, Torriani, & Herold, 2006). However, since the sites are
159 rather small (Moossee: 0.31 km^2, Burgäschisee 0.21 km^2), we assume that the pollen source

area only spans several hundred meters to at most a few kilometers (Conedera, Tinner, Crameri, Torriani, & Herold, 2006; Sugita, 1994).

Samples for macrofossil analyses (including macroscopic charcoal) had mean volumes of 17.5 cm^3 (Moossee) and 11 cm^3 (Burgäschisee) and were sieved with a mesh size of 200 µm. Terrestrial remains (e.g. *F. sylvatica* bud scales) were identified under a stereo microscope. Macrofossil concentration (remains cm^{-3}) were calculated and plotted in Figures 3 and 4. Plant macrofossils mainly indicate local vegetation as a result of short dispersal distances (1−100 m; Birks, 2003).

Microscopic charcoal particles >10 µm and <500 µm were counted on pollen slides following Tinner and Hu (2003) and Finsinger and Tinner (2005) and presented as microscopic charcoal influx values (particles cm^{-2} $year^{-1}$; Figures 3 and 4). These values were used as a proxy for regional fire activity since microscopic charcoal particles are dispersed over distances of *c.* 20-50 km (Adolf et al. 2018; Tinner et al. 1998).

Macroscopic charcoal pieces >600 µm were identified under a stereo microscope during macrofossil analysis. Their occurrence (pieces cm^{-3}) may primarily reflect local fire activity within few hundred meters distance (Adolf et al., 2018; Figures 3 and 4). This procedure (large sampling volume, size threshold >600 µm) allows reducing the influence of regional fires on macroscopic charcoal, without using de-trending and peak isolation approaches (Adolf et al., 2018).

Green algae (*Botryococcus*, *Tetraedron*, *Coelastrum*) and akinetes of cyanobacteria (*Anabaena*, *Aphanizomenon*) were counted on pollen slides to estimate changes in the trophic levels. Although, single NPP taxa might occur under natural conditions, contemporaneous or consecutive high numbers of green algae and cyanobacteria are considered as a proxy for eutrophication during or after local anthropogenic impacts (van Geel, Mur, Ralska-

Jasiewiczowa, & Goslar, 1994; Hillbrand, van Geel, Hasenfratz, Hadorn, & Haas, 2014). All NPPs are presented as percentages of the terrestrial pollen sum (Figures 3 and 4).

Local pollen assemblage zones (LPAZ; Figures 3 and 4) were delimited using optimal sum-of-squares partitioning (Birks & Gordon, 1985) with the program ZONE 1.2 (Juggins, 1991). Statistically significant zones were assessed with the program BSTICK (Line & Birks, unpublished software) following the broken-stick method (Bennett, 1996). The programs Tilia 2.0.41 and CorelDraw were used to plot the data for both high-resolution sequences (Figures 3 and 4).

2.4. Biodiversity estimations

Rarefaction analysis was used to calculate the palynological richness (PRI), which is commonly used as a proxy for species richness at local to regional scale in many palaeoecological studies (e.g. Birks & Line, 1992; Colombaroli & Tinner, 2013; Odgaard, 1999; Schwörer, Colombaroli, Kaltenrieder, Rey, & Tinner, 2015). Rarefaction analysis allows estimating the number of taxa per sample for a constant counting sum (Birks & Line, 1992), which was 500 at both sites. The probability of interspecific encounter (PIE; Hurlbert, 1971) was used as a measure of palynological evenness. In previous studies PIE was used to evaluate effects of few dominant pollen producers (e.g. *C. avellana*; van der Knaap, 2009) on the palynological assemblages and in particular on palynological richness. To assess such effects, PIE-derived evenness-detrended palynological richness (DE-PRI) was calculated following Colombaroli, Beckmann, van der Knaap, Curdy, and Tinner (2013). This approach aims at removing the evenness trend from palynological richness by building an ordinary least square regression (OLS) between the dependent (PRI) and the independent variable (palynological evenness). The resulting residuals of pollen richness (= PRI - PIE) are then distributed around the original pollen richness

values (Colombaroli & Tinner, 2013). Only if PRI and DE-PRI show similar changes and trends, we assume that the species richness estimates are unaffected by evenness effects. The DE-PRI approach has proven to be valuable to estimate contemporary species richness patterns at the European scale (Adolf, 2017). The program R statistics (R Development Core Team, 2016) was used for all calculations (see results in Figures 3 and 4).

2.5. Time-series analyses (cross-correlations)

Cross-correlations (Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Green, 1981; Rey et al., 2013; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999) were calculated to identify leads and lags between fire (microscopic charcoal influx values) and vegetation (pollen percentages, PRI, PIE, DE-PRI) by using the program MYSTAT 12 (Systat, 2007). The time window for all calculations was 6,500−4,150 cal year BP that included 209 samples at Moossee (1 sample = 11.1 ± 0.2 cal years) and 266 samples at Burgäschisee (1 sample = 8.7 ± 0.6 cal years). Cross-correlation coefficients for microscopic charcoal influx values vs. pollen percentages, PRI, PIE and DE-PRI (see Figure 5) were calculated at ±50 lags corresponding to ±555 cal years (Moossee) and ±435 cal years (Burgäschisee), following Bahrenberg, Giese, Mevenkamp, and Nipper (2008), with maximum lag numbers corresponding to one fourth of the sample number N (lag number ≤ N/4). The correlation coefficients at lag 0 between microscopic charcoal and selected pollen types are represented as detailed correlograms (Figure 6). For cross-correlation analyses between the two sites (e.g. *F. sylvatica* percentages at Moossee vs. *F. sylvatica* percentages at Burgäschisee), the time series with higher time resolution (Burgäschisee) was adjusted to the one with lower resolution (Moossee) by combining neighbouring samples following Tinner et al. (2015). This led to a total of 209 samples (1 sample = 1 lag = 11.1 ± 0.2 cal years) and ±50 lags (= ±555 cal years) that were

included in the cross-correlation calculations (Figure 7). Variables were not de-trended prior to the cross-correlation analyses because the vegetation type remains more or less uniform for the whole time window without pronounced population trends (see Figures 3 and 4; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). The 95% (2σ) confidence intervals of the correlations were estimated by computing ±2 standard errors of the correlation coefficients (Bahrenberg, Giese, Mevenkamp, & Nipper, 2008). This corresponds to a two-sided significance level (α) of 5% (Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999).

3. RESULTS

3.1. Vegetational, agricultural and fire dynamics

Both studied pollen records (Moossee: 7,000–3,900 cal year BP, Burgäschisee: 6,500–3,800 cal year BP) have a high temporal resolution of *c.* 10 cal years per sample and an extraordinary chronological precision (Rey et al., 2018). Zonation analyses show a high number of significant LPAZ (Moossee: 15, Burgäschisee: 14; see Figures 3 and 4), suggesting high variability of vegetation composition over time. In general, *F. sylvatica* was dominant in the closed forests (pollen percentages generally ≥20%). This pollen-based interpretation is supported by regular finds of macrofossils (bud scales). Other important taxa in the forests included *Quercus* and *A. alba*. The latter shows slightly higher pollen percentages at Burgäschisee (up to 10% instead of 5%), probably as a result of increasing precipitation towards the east of the Swiss Plateau, making the species more competitive under mesophilous conditions (Rey et al., 2017). However, macrofossil and stomata finds of *A. alba* point to local occurrences of the species at both sites. *Alnus glutinosa* was preferably growing on the wet soils at the lake shores as indicated by high and fairly stable pollen percentages (around 25%) and abundant macrofossils finds (e.g. *A. glutinosa* fruits). Pollen percentages of other subordinate taxa such

as *Tilia*, *Ulmus* and *Taxus baccata* steadily decrease until *c.* 5,000 cal year BP after which they remain low (<2%, see *Ulmus*) or even disappear (see *Tilia* and *T. baccata*), most likely as a result of overexploitation and fire disturbance (Rey et al., 2017; Tinner, Conedera, Ammann, & Lotter, 2005). Distinct phases with low *F. sylvatica* pollen percentages (<10%), increased cultural indicators (Cerealia-type, *Plantago lanceolata*, *Linum usitatissimum*-type), apophytes (*Urtica*), other herbs (Poaceae, *Allium*-type) and heliophilous shrubs (*C. avellana*, *Juniperus*) are apparent at both sites. A first phase is dated at 6,550−6,150 cal year BP at Moossee and at 6,300–5,950 cal year BP at Burgäschisee. Subsequently, similar phases occurred at 5,750–5,550 cal year BP, at around 5,400 cal year BP and at 5,100–4,600 cal year BP at both sites. Finally, a last phase is dated around 3,900 cal year BP at Moossee. Periods of forest disruption were generally accompanied by high regional fire activity as suggested by increasing microscopic charcoal influx values (>5,000 particles cm^{-2} yr^{-1}), sometimes overlapping with local fire activity as inferred from macroscopic charcoal presence (≥600 µm). This finding is in good agreement with local archaeological evidence (e.g. pile dwellings, light grey bars in Figures 3 and 4). Some settlements around the lake had impacts on the water quality as shown by high numbers of cyanobacteria (*Anabaena*, *Aphanizomenon*) and green algae (*Tetraedron*) between 5,750 and 5,550 cal year BP at both lakes and around 4,600 cal year BP at Moossee. Such blooms are best explained by strong lake water eutrophication. After the settlement phases, *Betula* as a pioneer tree species quickly recolonized abandoned places (pollen percentages up to 30% and abundant macrofossils). After intermediate phases often with *F. excelsior, Ulmus* and *Tilia* expansions, these trees were unremittingly replaced within 150–200 years by late successional tree species (*F. sylvatica*, *A. alba*) if no further disturbances occurred. These succession cycles were simultaneously repeated at both sites and are not only

visible in the pollen percentage data but are also confirmed by plant macrofossils, indicating possible broad-scale succession trajectories.

3.2. Biodiversity reconstruction

Palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI) show good agreements (Figures 3 and 4), suggesting that overall trends in palynological richness are not strongly affected by evenness. PRI and DE-PRI generally increase during phases with higher human impact (>25 pollen types per sample), i.e. around 6,400 cal year BP, 4,600 cal year BP and 3,900 cal year BP at Moossee, at 5,700–5,600 cal year BP at both sites, and around 4,900 cal year BP at Burgäschisee. These increases are directly related to vegetation openings and the introduction of cultivated plants (*Hordeum*-type, *Triticum*-type, *L. usitastissimum*-type). The establishment of open land for Neolithic farming created new habitats for short-lived weeds (*P. lanceolata*), apophytes (*Urtica*) and light-demanding shrubs (*C. avellana*, *Sambucus nigra*). Palynological evenness as inferred from PIE (Figures 3 and 4) is more or less stable (PIE around 0.85). Slightly lower values of palynological evenness (PIE around 0.8) are recorded in phases when either *Betula* or *F. sylvatica* pollen grains are dominant and the forests were rather closed, suggesting that the expansion of monospecific stands may have affected species evenness. On the other hand, phases with open forests (e.g. 5,700–5,600 cal year BP at both sites) have usually high palynological evenness values (PIE ≥0.85), suggesting that vegetation evenness is correlated to openness.

3.3. Time-series analyses

At both sites, pollen percentages of trees have significant negative correlations with microscopic charcoal influx (maximum negative correlations at lag 0; Figure 5). *F. excelsior* is

303 a good example to illustrate immediate negative fire impacts. The negative correlations of *F.*
304 *sylvatica* pollen percentages is, however, markedly delayed at both sites (*c.* 320 years after a
305 fire at Moossee respectively *c.* 80 years after a fire at Burgäschisee), possibly indicating a
306 slightly higher fire tolerance compared to other tree species (Tinner et al., 2000). On the other
307 hand, pollen percentages of herbs (e.g. Cerealia-type) reach maximum positive correlations
308 with microscopic charcoal at lag 0, showing that agropastoral activities were strongly
309 connected to the use of fire. Similarly, correlations between microscopic charcoal influx and
310 PRI, DE-PRI and at Moossee also PIE suggest that biodiversity increased in the new habitats
311 (i.e. open areas) created by anthropogenic burning for agricultural purposes. Pollen
312 percentages of shrubs such as *C. avellana* and *Salix* also have significant positive correlations,
313 e.g. at Burgäschisee maximum positive correlations are reached at lag +4 for *C. avellana* (*c.* 35
314 years after a fire) and at lag 0 for *Salix* (Figure 5b). *Betula* shows maximum positive correlations
315 at lag +35 (*c.* 390 years after a fire; Figure 5a) at Burgäschisee and at lag +41 (*c.* 355 years after
316 a fire; Figure 5b) at Moossee. This result with *C. avellana* preceding *Betula* pollen percentages
317 is likely caused by the successional trajectories after fire disturbance. Later on, the recovery
318 of *F. excelsior* follows (lag +41 and lag +45, corresponding to *c.* 455 and *c.* 390 years) after the
319 fire-related decline (negative correlations) as well as *F. sylvatica* (lag +50 = *c.* 435 years; Figure
320 5b). Correlation coefficients at lag 0 between microscopic charcoal influx values and pollen
321 types or PRI, PIE and DE-PRI show similar linkages (Figure 6), with significant positive
322 correlations for cultural indicators (*Hordeum*-type, *Triticum*-type), other herbs (e.g. *Allium*-
323 type, *Mentha*-type, *Papaver rhoeas*-type, *Urtica*), PRI, DE-PRI and shrubs (e.g. *C. avellana*,
324 *Salix*, *S. nigra*). In contrast, most tree pollen types (e.g. *Quercus*, *F. excelsior*, *F. sylvatica*,
325 *Ulmus*, *T. baccata*) have significant negative correlations with microscopic charcoal,
326 suggesting that forest trees were most affected by anthropogenic burning. However, *A.*

glutinosa-type as an important tree pollen type is indifferent showing neither significant positive nor negative correlations with charcoal-inferred fire incidence.

If cross-correlations are used to compare the two sites, a striking pattern appears (Figure 7). Total shrubs and trees as well as some taxa (e.g. *C. avellana*, *Betula*, *F. sylvatica*, *Tilia*) show pronounced positive correlations with maximum correlations at lag 0, suggesting synchronous oscillations within the pooled sample resolution (11.1 ± 0.2 cal years). Cross-correlations between pollen percentages of herbs (Moossee data vs. Burgäschisee data), *F. excelsior* and *A. alba* only slightly differ and may reflect local vegetation variability, however, significant positive correlations also center around lag 0 with maximum positive correlations within *c.* ±35 years. Of particular interest are the correlations for the cereals, that also show this pattern, confirming that the cultural phases at the two sites were largely coeval with only minor differences, possibly indicating positive synergy effects of cereal production in old and new prehistoric centres. Similarly, also PRI and DE-PRI co-vary in time at the two sites. Taken together, these results quantitatively show that the general succession patterns after disturbance were not only similar as presented in Figures 3 and 4 but in fact synchronous at the two sites.

4. DISCUSSION

4.1. Impacts of land-use on temperate forests and synchronous patterns of forest succession after disturbances

The palaeobotanical data suggest the dominance of mixed beech forests over millennia at our two study sites Burgäschisee and Moossee. Land-use phases contributed to openings and a gradual conversion from mixed beech to almost pure beech forests. These general patterns have been observed elsewhere in the lowlands of southern Central Europe after *c.* 7,000 cal

year BP (e.g. Ammann, 1989; Kleinmann, Merkt, & Müller, 2015; Rösch & Lechterbeck, 2015; Tinner & Ammann, 2005; Tinner, Conedera, Ammann, & Lotter, 2005). However, local differences in species composition resulted from dissimilar environmental conditions. For instance in Switzerland, moisture availability increases towards higher elevations and to the east. This moisture gradient may have led to the co-dominance of *A. alba* in the forests (Gobet & Tinner, 2012; van der Knaap, van Leeuwen, & Ammann, 2004; Lotter, 1999; Wehrli, Tinner, & Ammann, 2007), given that as the most shade tolerant and tallest tree species of Europe, silver fir is particularly competitive under mesophilous conditions (Ellenberg, 2009; Ruosch et al., 2016; Tinner et al., 2013). Conversely, drier conditions in the Lake District (Seeland) in the rain shadow of the Jura Mountains may have promoted *Quercus* spp. including submediterranean *Q. pubescens* (Ammann, 1989; Hadorn, 1992; Steiger, 2010).

Several diebacks of mixed *F. sylvatica* forests occurred between 6,400 and 6,000 cal year BP, at 5,800–5,650 cal year BP, 5,400–5,300 cal year BP, at 5,100–4,700 cal year BP at both sites and around 3,900 cal year BP at Moossee only. The combined charcoal and pollen evidence as well as the cross-correlation analyses suggest that burning was used as a tool for opening the mixed *F. sylvatica* forests, creating a mosaic of new habitats that advantaged many herbaceous species, increasing the overall biodiversity (see biodiversity estimations in Figures 3 and 4). A similar pattern has been reconstructed in previous studies and might be typical for European landscapes (Colombaroli, Beckmann, van der Knaap, Curdy, & Tinner, 2013; Colombaroli & Tinner, 2013; Giesecke, Ammann, & Brande, 2014). Prehistoric slash-and-burn activities were strong enough to release a wide-scale expansion of early-successional shrublands, typically dominated by *C. avellana*, *Betula* and *Alnus* (Aaby, 1986; Tinner, Conedera, Ammann, & Lotter, 2005; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). In contrast, most tree species were strongly reduced by fires and other human disturbances

such as logging, pollarding and browsing (e.g. Haas, Karg, & Rasmussen, 1998; Haas & Schweingruber, 1993; Pott, 1985; Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). Most interestingly, some tree species such as *F. sylvatica* and *A. alba* seem to have fully recovered and even expanded after forest disruptions (within *c.* 150–200 years after a land-use phase), suggesting long-term resilience to moderate human disturbance, while others (*Ulmus*, *Tilia*, *Acer* and *T. baccata*) markedly diminished, suggesting high sensitivity of these species. Ultimately, at *c.* 5,000 cal year BP (Figure 3 and 4) this process of repeated disturbances led to a strong impoverishment in species diversity of forest ecosystems (Tinner & Ammann, 2005), generating the advent of monospecific forests that are characteristic for Central European landscapes today (e.g. almost pure spruce, beech, larch, oak stands, depending on altitude and other environmental conditions; Ellenberg, 2009; Gobet, Vescovi, & Tinner, 2010).

Here, we quantitatively demonstrate for the first time that forest succession cycles over 3,000 years were regionally synchronous (Figure 7). The distance between the two sites (*c.* 25 km) exceeds the expected pollen catchment expected for the two study sites (most pollen from within a few hundred meters to at most a few kilometers; Conedera, Tinner, Crameri, Torriani, & Herold, 2006), arguing for coeval population dynamics over the millennia within the time resolution and precision available (*c.* 20−50 cal years; Rey et al., 2018). Because this pattern was found in the cross-correlation analyses for several tree taxa as well as for the tree percentage sum, we consider it to be very reliable. Synchronous forests disruptions (tree pollen <80%) may have occurred at several distant sites in Central and Southern Europe (Figure 8). The few available high-resolution (*c.* 10−20 years) and high-precision (sufficient radiocarbon dates on terrestrial material) time series covering the entire Neolithic and the onset of the Bronze Age reveal coeval tree population reductions at *c.* 6,400–

399 5,900 cal year BP, 5,750–5,600 cal year BP, 5,400 cal year BP, 5,100–4,700 cal year BP and
400 around 3,900 cal year BP (Ammann, 1989; Kleinmann, Merkt, & Müller, 2015; Lotter, 1999;
401 Rösch, Kleinmann, Lechterbeck, & Wick, 2014a, b; Tinner, Hubschmid, Wehrli, Ammann, &
402 Conedera, 1999; Wehrli, Tinner, & Ammann, 2007). One of these sites, Lago di Origlio, is
403 located in the lowlands south of the Alps (Sottoceneri), where environmental conditions are
404 typical for submediterranean Southern Europe (warmer summers, milder winters). We thus
405 hypothesize the existence of supra-regional synchronicity of forest disturbances during the
406 Neolithic, as it was formerly advocated for Central and Southern Europe (including Sicily) for
407 the Bronze Age, the Iron Age, the Roman Period and the subsequent early medieval times
408 (Finsinger & Tinner, 2006; Gobet, Tinner, Hochuli, van Leeuwen, & Ammann, 2003; Tinner et
409 al., 2003, 2009).
410
411 **4.2. Possible impacts of climate on land-use phases**
412 Simultaneous broad-scale deforestation phases over large areas caused by land-use may
413 mainly reflect superimposed causes such as climate change (e.g. Berglund, 2003; Tinner et al.,
414 2003, 2009). Our study sites showing coeval vegetation succession patterns are both located
415 in landscapes providing fertile arable lands (Guthruf, Zeh, & Guthruf-Seiler, 1999). They are
416 mostly lacking major in- and outflows, thus settlements around the lakes, especially at the
417 shores (e.g. pile dwellings) may have been affected by lake level changes (Guthruf, Zeh, &
418 Guthruf-Seiler, 1999). We here assume that people settled at lower elevations preferably near
419 lake shores/rivers during warm and dry phases and subsequently moved upwards to slightly
420 higher elevations during cool and wet phases. Thus, the more densely populated warm and
421 dry phases might be preferentially reflected in the archaeological and dendrochronological
422 records e.g. at Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter,

2000; Stöckli, 2016; Suter, 2017) and Lake Zurich (Bleicher et al., 2017), whereas the fewer settlements on dry soils during cool and wet phases (e.g. hilltop sites) were more exposed to erosion, hence artifacts are scarce.

Common land-use phases across Central and Southern Europe were possibly driven by temperature oscillations, which were usually associated with moisture changes. After 8,200 cal year BP, warm periods in and around the Alps were generally associated with dry conditions, while decadal to centennial scale cold excursions were wetter, comparable to the conditions during the Little Ice Age (Haas, Richoz, Tinner, & Wick, 1998; Tinner & Lotter, 2006). Indeed wet phases, as reconstructed from lake-level proxies occurred at around 6,300, 5,500 and 4,200 cal year BP (Magny, 2004, 2013), when crop production around the lakes was low. The linkage to warm phases as reconstructed from tree-ring records (Bircher, 1982, 1986; Renner, 1982) and the Greenland stable oxygen isotope records (Vinther et al., 2006) is less pronounced (Figure 9). Although the Swiss tree-ring records of temperature change are well in line with the Greenland stable oxygen isotope record, the chronological precision of these records (*c.* ±50–100 cal years) is lower than that of the dendrochronologically dated archaeological evidence (*c.* ±5–10 years). Previous studies have emphasized the good match between the dendrochronologically dated archaeological phases and solar activity, as reconstructed from the ^{14}C-residuals at multiannual to multidecadal scales (Gross-Klee & Maise, 1997; Kleinmann, Merkt, & Müller, 2015; Magny, 2004, 2013). The link between solar activity and archaeological evidence becomes again evident when comparing the land-use phases at both study sites with the reconstructed average total solar irradiance (TSI; Steinhilber, Beer, & Fröhlich, 2009; see Figure 9). Periods with high solar irradiance corresponded with rather dry conditions (low lake levels) and increases of cultural indicators (sum of cereals, *L. usitatissimum*, *P. lanceolata*), local–regional fires (macroscopic and

447 microscopic charcoal) and biodiversity (PRI). Conversely, periods with lower TSI and wetter
448 conditions (high lake levels) corresponded to land abandonment phases. We assume that
449 under adverse wet and cool conditions agricultural yields collapsed and human population
450 densities declined over large areas, as shown by the excellent agreement across distant sites
451 (Figure 8). Solar irradiance may have additionally advantaged crop production, given that the
452 cereals, which were the main source of calories, originate from the Near East and are adapted
453 to high insolation.
454

455 **4.3. Implications for global change ecology**

456 Our study shows that over the millennia temperate forests dominated by *F. sylvatica* and *A.*
457 *alba* were resilient to prehistoric human impacts in the Swiss Plateau. Forest succession after
458 disturbances generally started with light-loving pioneer species (*C. avellana*, *Betula*) and was
459 completed within 150–200 years by late successional mixed beech forests. Such
460 palaeoecological information might be crucial to develop sustainable strategies for nature
461 conversation and forest management (Feurdean & Willis, 2008; Lindbladh, Niklasson,
462 Karlsson, Björkman, & Churski, 2008; Valsecchi, Carraro, Conedera, & Tinner, 2010),
463 specifically under global-change conditions that are currently releasing forest ecosystem
464 expansions in abandoned rural areas (FOREST EUROPE, 2015). We assume that *F. sylvatica*
465 forests will remain key communities in Central Europe, if future (summer-) climate warming
466 does not exceed the Holocene variability range (*c.* +1–2°C compared to the 20th century; Heiri,
467 Tinner, & Lotter, 2004). Other trees such as *F. excelsior*, *Tilia* and *Ulmus* might also re-expand
468 under low disturbance levels (e.g. no browsing, no pollarding) provided that no further
469 devastating diebacks due to pathogenic diseases (e.g. *Ulmus*, *F. excelsior*) occur (see Brasier,
470 1991; McKinney, Nielsen, Hansen, & Kjær, 2011). Anticipated climate change (Appenzeller et

al., 2011; Kovats et al., 2014), however, with generally lower annual precipitation rates may markedly disadvantage *F. sylvatica* and promote *A. alba* and *Quercus* spp. (including submediterranean *Q. pubescens*) that are less-drought sensitive and thus more competitive under drier conditions (Bugmann et al., 2015; Ellenberg, 2009; Ruosch et al., 2016; Tinner et al., 2013). Predicted higher risk of forest fires (Kovats et al., 2014) may affect fire-sensitive *A. alba* (Tinner et al., 2013), or conversely *A. alba* and the expansion of mediterranean evergreen trees (e.g. *Quercus ilex*) may further reduce fire incidence because of positive feedbacks mainly related to decreased biomass flammability (Henne et al., 2015, 2018).

5. CONCLUSIONS

We numerically demonstrate for the first time that vegetation dynamics at two distant sites were synchronous over more than 2,000 years, with a pooled sampling resolution of 11 years. Interactions between the first agrarian societies and their environment were complex, with humans significantly shaping vegetation structure (creation of open land, shrublands) and composition (shift in species). Conversely, the rise and fall of early farming societies was likely dependent on climate. Favourable climatic conditions (i.e. warm and dry summers) probably led to an increase in agricultural yields, the expansion of farming activities and resulting forest openings, whereas unfavourable climatic conditions (i.e. cold and wet summers) likely caused crop failures, abandonment of agricultural areas and forest succession. A better understanding of the environmental and societal factors controlling coeveal land-use dynamics as shown in this study would require new climate proxy data (e.g. temperature reconstruction from well dated and complete Holocene tree ring series). On the basis of our results and considering the ongoing spread of temperate forests in lowland Central Europe, we conclude that the existing beech forest ecosystems are resilient to anthropogenic

disturbances under a changing climate, if the amplitude does not exceed the range of Holocene climate variability. Our results also indicate that abandoned agricultural land can revert to quasi-natural mixed beech forests within 150–200 years. Climate warming exceeding the Holocene variability range, however, has been identified as an important threshold that might cause the rapid collapse of beech forests, giving way to novel communities that are today restricted to Southern Europe.

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AUTHORS' CONTRIBUTIONS

F.R. performed all pollen, macrofossil and quantitative analyses, figure construction, and led the writing; E.G. and W.T. initiated and designed the research project and wrote substantial parts of the manuscript; C.S. helped to conduct the biodiversity estimations; A.H. and O.W. provided archaeological data; W.T. and A.H. obtained funding. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The data will be available through the Alpine Palynological Database (ALPADABA) after publication.

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FIGURES

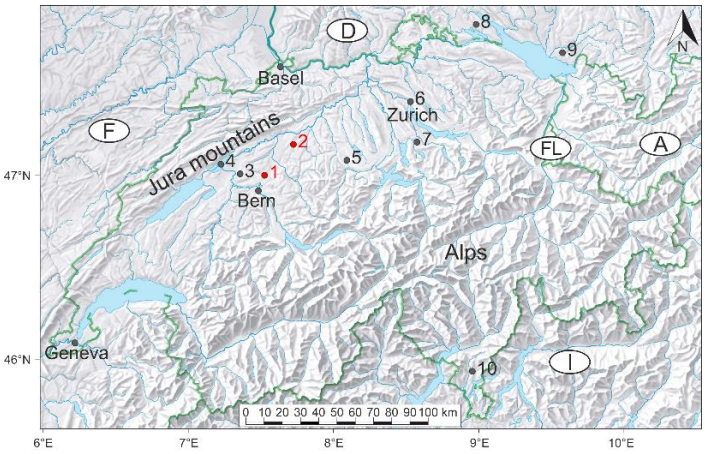

FIGURE 1 Overview map of Switzerland and the neighbouring countries with the two sites of this study (in red) and other discussed sites. 1 Moossee; 2 Burgäschisee; 3 Lobsigensee (Ammann, 1989); 4 Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter, 2000; Stöckli, 2016; Suter 2017); 5 Soppensee (Lotter, 1999); 6 Zürich Opéra (Bleicher et al., 2017); 7 Egelsee (Wehrli, Tinner, & Ammann, 2007); 8 Mindelsee (Rösch, Kleinmann, Lechterbeck, & Wick, 2014a, b); 9 Degersee (Kleinmann, Merkt, & Müller, 2015); 10 Lago di Origlio (Tinner, Hubschmid, Wehrli, Ammann, & Conedera, 1999). A = Austria, D = Germany, F = France, FL = Liechtenstein, I = Italy (topographic map: © swisstopo)

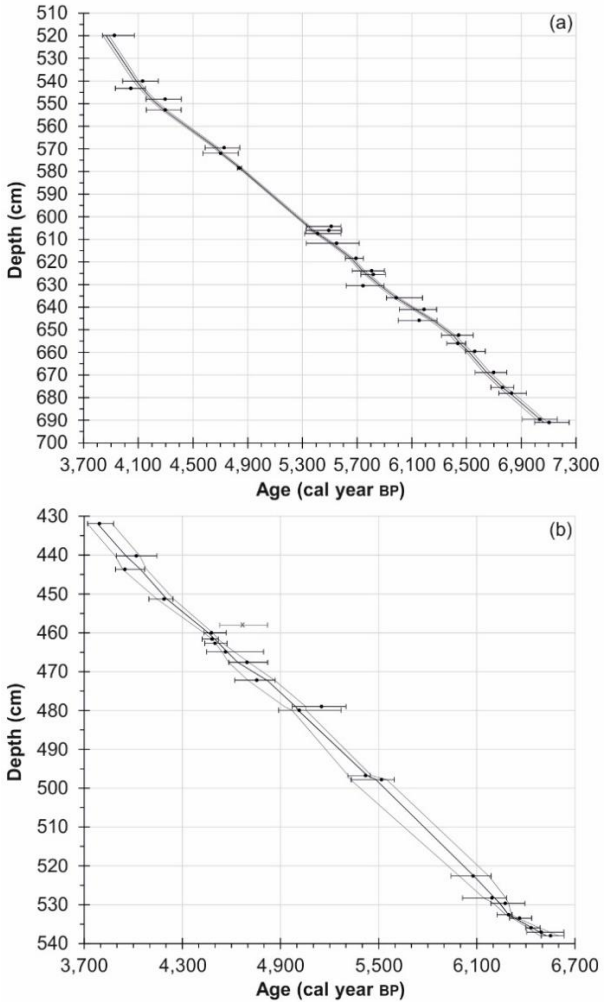

FIGURE 2 Age-depth models of (a) Moossee and (b) Burgäschisee. Black dots show the calibrated ages with 95% (2σ) probabilities (IntCal13, Reimer et al., 2013). The black lines are the modelled chronologies (OxCal; Bronk Ramsey, 1994, 1995, 2001, 2008; Bronk Ramsey, van der Plicht, & Weninger, 2001; Bronk Ramsey & Lee, 2013). One age at Burgäschisee (dark grey x) was treated as an outlier. The grey lines indicate the 95% (2σ) probabilities of the models.

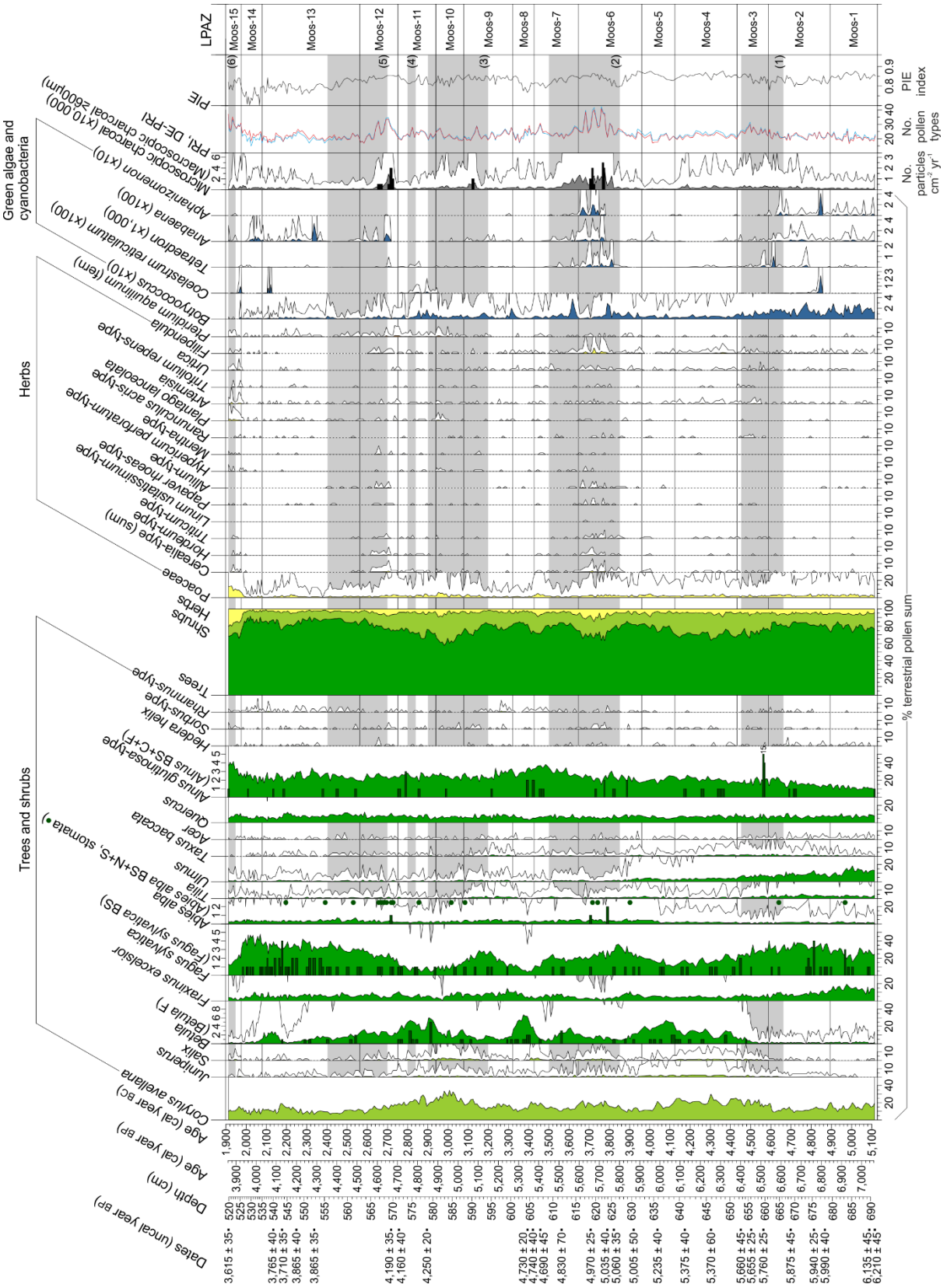

FIGURE 3 Moossee high-resolution sequence. Presented are selected pollen, spore, algae and cyanobacteria percentages, microscopic charcoal influx values, macroscopic charcoal concentrations (concentration = number of particles ≥600 µm/17.5 cm³, black bars, plotted on top axis), selected plant macrofossil concentrations (concentration = number of remains/17.5 cm³, dark green bars, plotted on top axis), presence of *Abies alba* stomata (dark green dots), palynological richness (PRI, light blue), evenness-detrended palynological richness (DE-PRI, red) as well as palynological evenness (PIE). Empty curves show 10× exaggerations. Light grey bars indicate the time windows of local archaeological findings reflecting settlement phases (1–6). BS = bud scales, C = cones, F = fruits, N = needles, S = seeds.

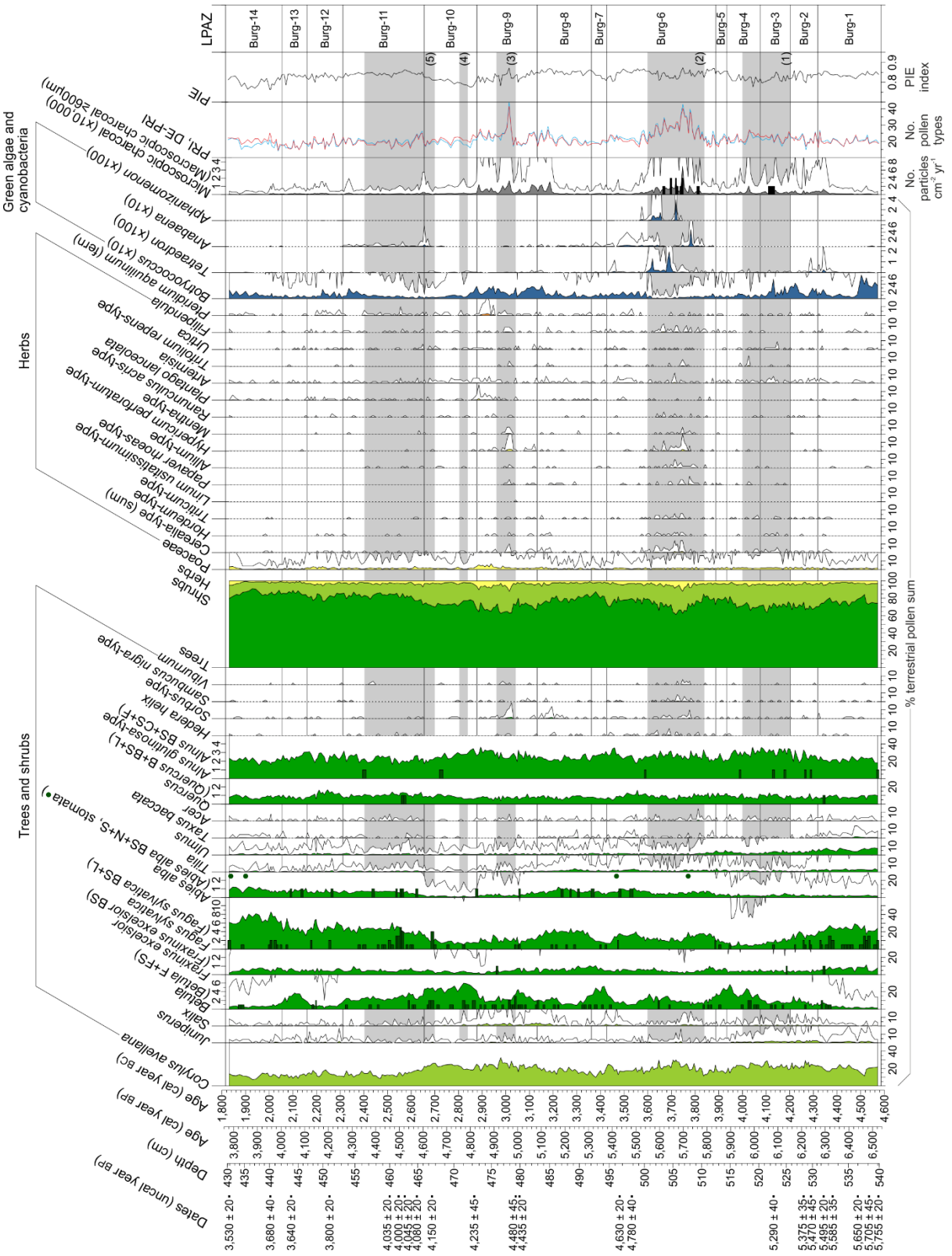

FIGURE 4 Burgäschisee high-resolution sequence. Presented are selected pollen, spore, algae and cyanobacteria percentages, microscopic charcoal influx values, macroscopic charcoal concentrations (concentration = number of particles ≥600 µm/11 cm^3 (standard volume), black bars, plotted on top axis), selected plant macrofossil concentrations (concentration = number of remains/11 cm^3 (standard volume), dark green bars, plotted on top axis), presence of *Abies alba* stomata (dark green dots), palynological richness (PRI, light blue), evenness-detrended palynological richness (DE-PRI, red) as well as palynological evenness (PIE). Empty curves show 10× exaggerations. Light grey bars indicate the time windows of local archaeological findings reflecting settlement phases (1–4). B = bud, BS = bud scales, CS = cone scales, F = fruits, FS = fruit scales, L = leaves, N = needles, S = seeds.

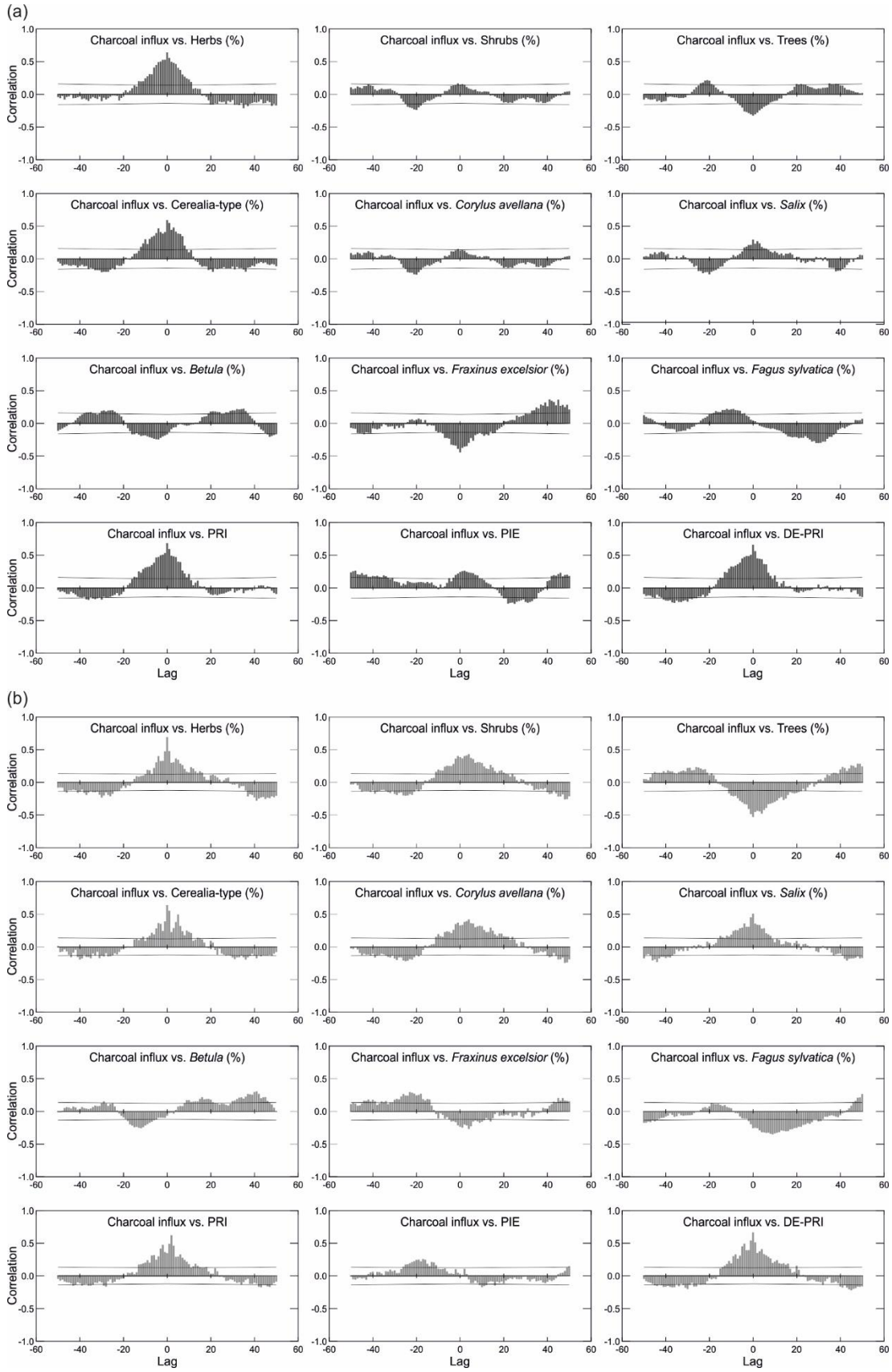

FIGURE 5 Cross-correlation analysis of microscopic charcoal influx vs. percentages of selected pollen types, palynological richness (PRI), palynological evenness (PIE) and evenness-detrended palynological richness (DE-PRI) from (a) Moossee and (b) Burgäschisee (6,500−4,150 cal year BP). 1 lag = 11.1 ± 0.2 cal years (Moossee), 8.7 ± 0.6 cal years (Burgäschisee). The solid black lines mark the significance level ($P < 0.05$).

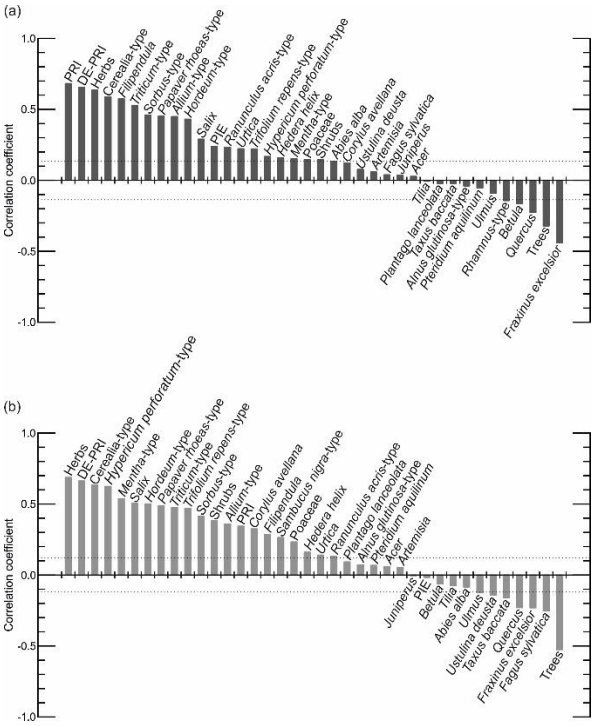

FIGURE 6 Correlograms showing the correlation coefficients at lag 0 between microscopic charcoal influx and selected pollen types, spore types, palynological richness (PRI), palynological evenness (PIE) and evenness-detrended palynological richness (DE-PRI) for (a) Moossee and (b) Burgäschisee (6,500−4,150 cal year BP). The dotted lines mark the significance level ($P < 0.05$).

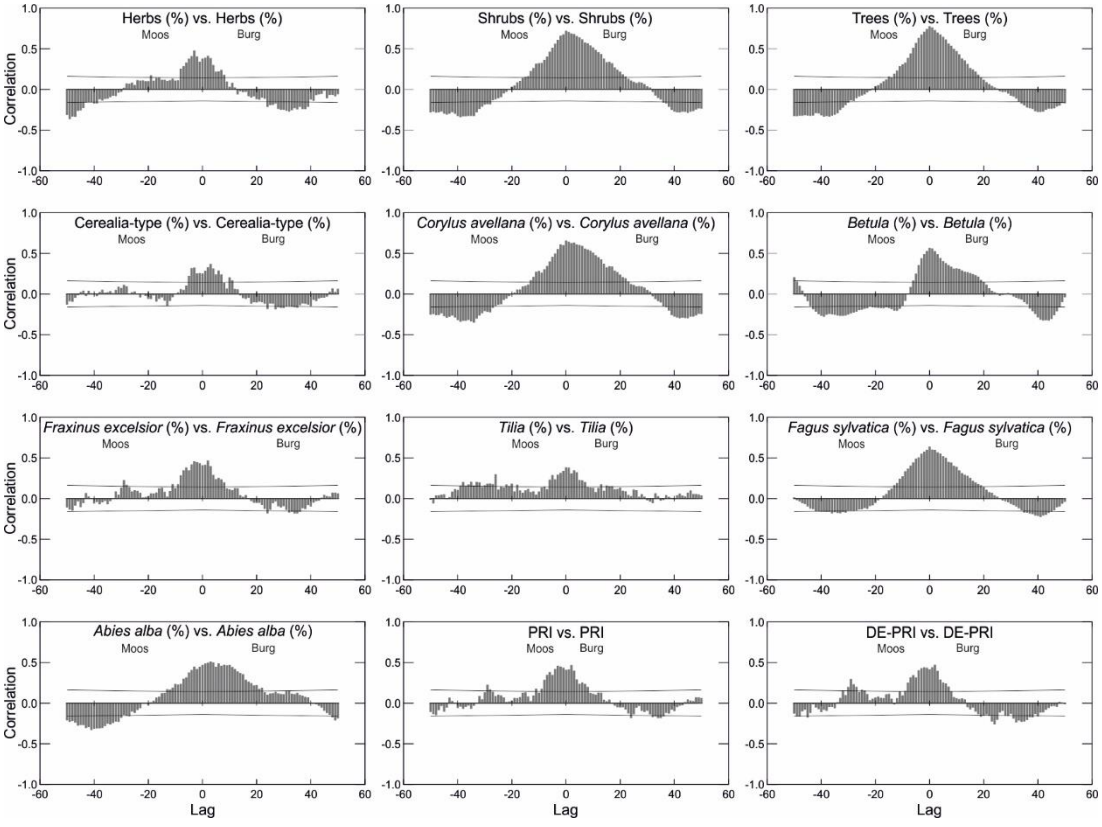

FIGURE 7 Cross-correlation analysis of percentages of selected pollen types, palynological richness (PRI) and evenness-detrended palynological richness (DE-PRI) from Moossee (Moos) vs. percentages of selected pollen types, PRI and DE-PRI from Burgäschisee (Burg) (6,500−4,150 cal year BP). 1 lag = 11.1 ± 0.2 cal. years. The solid black lines mark the significance level ($P < 0.05$).

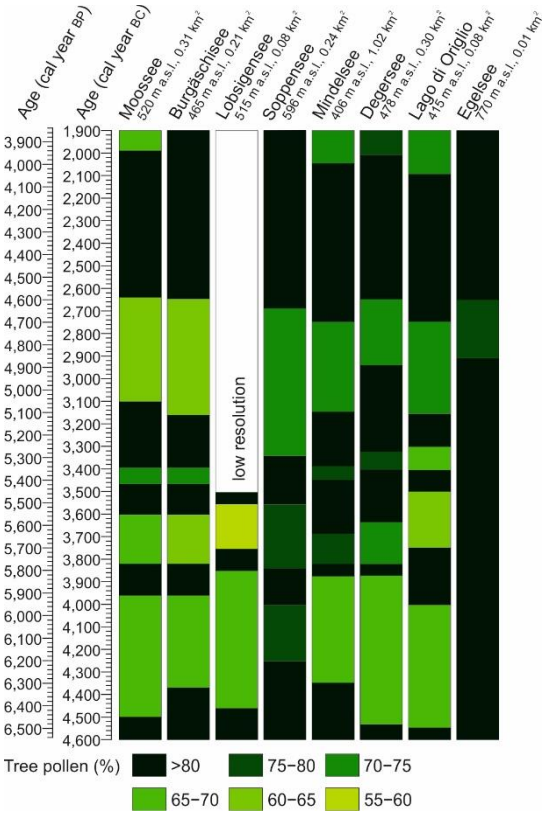

FIGURE 8 Tree pollen percentages from selected sites (see Figure 1). Dark green bars indicate periods with fairly closed forests (tree pollen % >80). Light green bars indicate phases with forest openings (tree pollen % <80).

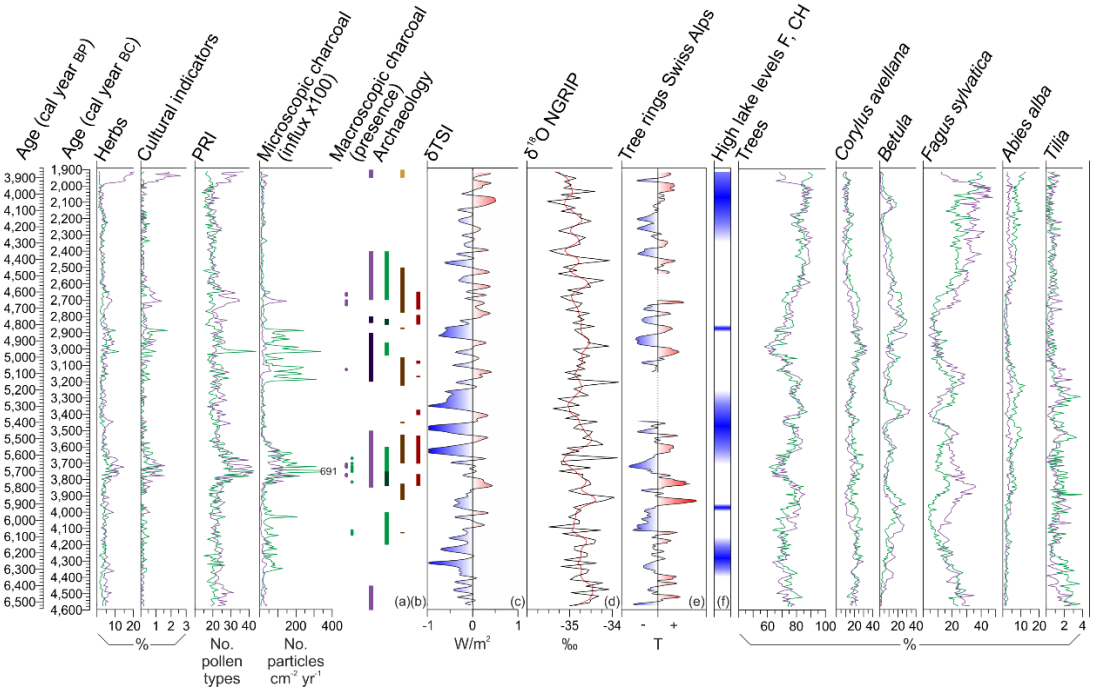

FIGURE 9 Percentages of selected pollen types, palynological richness (PRI), microscopic charcoal influx, macroscopic charcoal presence (≥600 µm) and local archaeological findings at Moossee and Burgäschisee compared to palaeoclimatic proxies. Purple graphs = Moossee, green graphs = Burgäschisee. Cultural indicators = ∑ Cerealia-type + *Plantago lanceolata* + *Linum usitatissimum*-type. Bottom labelling, center: (a) Local archaeological settlement phases within the city of Zurich (Bleicher et al., 2017). (b) Dendrochronologically dated settlement phases at Lake Biel (Fischer, Hafner, Stapfer, Marti, & Affolter, 2017; Hafner & Suter, 2000; Stöckli, 2016; Suter 2017). Dark coloured bars (archaeology) indicate dendrochronologically dated settlement phases (Moossee, Burgäschisee and Zurich). (c) δTSI (total solar irradiance) (Steinhilber, Beer, & Fröhlich, 2009). (d) $\delta^{18}O$ NGRIP (Vinther et al., 2006) with smoothing (loess = 0.05, red line). (e) Calibrated tree ring data from the Swiss Alps (Bircher, 1982, 1986; Renner, 1982). Dotted black lines mark data gaps (f) Periods of high lake levels in Eastern France (F) and Western Switzerland (CH) (Magny, 2004, 2013).